CHAPTER 13

Allelopathy: Adaptation or Accident?

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I. INTRODUCTION

If a plant produces a chemical which reaches another plant and affects its growth or metabolism, the phenomenon is called allelopathy. Normally the effect is harmful, but a beneficial effect is possible. Plants often compete for their basic requirements: light, water and mineral nutrients. If a plant can, by producing a toxic substance, reduce the growth of other plants in its vicinity, this is likely to increase the amount of these basic requirements available and so be an advantage to the plant producing the toxin. In this paper the plant producing the toxic substance is called the producer or donor, while the other plant whose response is monitored is called the receiver.

II. DOES ALLELOPATHY OCCUR?

The first key question is whether allelopathy actually operates in the field. If plant A is to reduce the growth of plant B by allelopathy:

1. Plant A must produce a toxic substance;
2. The substance must leave plant A.

3. The substance must reach plant B in sufficient concentration to influence its growth.

The first requirement is often met. Plants contain a tremendous variety of secondary compounds, many of them toxic to living things; some of them accumulate within the plant to substantial concentrations. Many examples are given elsewhere in this symposium volume. Del Moral and Cates (1971) tested 40 species growing in Washington state, U.S.A. for toxic materials; ferns, conifers and dicotyledons were included. They soaked bark or intact leaves in water and determined the effect of the extract on radicle elongation of *Hordeum vulgare*, *Bromus tectorum* and *Pseudotsuga menziesii*. The control solution was mannitol of equal osmotic potential to the extract. Every species provided an extract from either bark or leaf which was significantly inhibitory to at least one of the three receiver species and usually both bark and leaf extract were inhibitory. Inhibitory volatiles from chopped leaves were also produced by 36 out of the 40 species. Many other examples of inhibitory plant extracts are cited by Rice (1974), though the possibility that the effect is purely osmotic has unfortunately not always been checked.

The second requirement, that the substance leaves the donor plant, is also often fulfilled. Volatile materials can leave the aerial parts of plants; water-soluble materials can exude from the aerial parts and be washed off by rain, or can exude from the roots; leaves or twigs which fall from the plant may contain material which is subsequently released. Even if the substance is not released until the plant dies, this may still be important in determining what plant succeeds it at that site. Examples of all these methods by which substances leave the plant are given by Rice (1974).

It is more difficult to know the concentration of active substance which actually reaches the receiver plant. Although a toxin from the leaves of one plant may pass as a volatile or by rain-drip directly on to another plant, it is more usual for the substance to pass first into the soil. Here, depending on its properties, it may be rapidly leached out or may accumulated by adsorption. Del Moral and Muller (1970) showed that volatile terpenes from leaves of *Eucalyptus camaldulensis* were adsorbed by soil, making it toxic to various grass species. Soil taken from under the *Eucalyptus* trees in the field was shown to contain toxic concentrations of the terpenes. Toxic materials in soil may also be inactivated by micro-organisms. Haider and Martin (1975) and Martin and Haider (1976) added ^{14}C-labelled phenolic acids to soil and measured the subsequent evolution of $^{14}CO_2$. After four weeks about 60–80% of the ring-carbons had been converted to CO_2. Between four and twelve weeks little further $^{14}CO_2$ was evolved and it was shown that (for a few of the phenolics, at least) half or more of the remaining ^{14}C had been incorporated into soil humus. Thus toxic substances can be detoxified partly by breaking them down and partly by incorporating them into inert humic material. A further complication is that substances non-toxic in the plant can be transformed by microbial activity into toxic substances in the soil. Cyanogenic compounds are one example discussed elsewhere in this volume (Jones *et al.*, Chapter 2). Lignin decomposition gives rise to phenolics (Kirk, 1971) and even cellulose can, in anaerobic conditions, give rise to toxic levels of organic acids (Lynch, 1976). The chemical changes undergone by toxic material in soil are thus complex, and may be rapid. Furthermore, direct determination of the active concentration of a chemical in soil presents serious technical problems. Some extractants commonly used to remove phenolics, for example, could break down humus and release phenolic material which was chemically inert in the native soil. All these complications make it very difficult to determine the actual concentrations reaching the receiver plant at any time. Thus it is relatively easy to demonstrate that a plant product is inhibitory to growth of seedlings on filter paper in a Petri dish; to demonstrate that the same substance has a significant effect in the field is much more difficult.

Much research has been directed towards demonstrating that a particular species does influence other plants by allelopathy under field conditions. The subject is covered at length in the book by Rice (1974) and more briefly in reviews by Muller (1966) and Muller and Chou (1972). Rather than discussing this subject again, I wish to consider other questions which have been less often discussed. For the remainder of this paper I shall adopt the view that on balance the evidence suggests that allelopathy does at least sometimes operate in the field.

III. DOES ALLELOPATHY BENEFIT THE PRODUCER SPECIES?

If a plant produces a substance which is as toxic to its own species as to other species growing nearby, it is unlikely that allelopathy will benefit the producer species. It is therefore of interest to know whether plants do produce chemicals which reduce the growth of their own species, i.e. whether species are autotoxic. Table I lists species whose extracts or exudates have been shown to be autotoxic. Response of the receiver plants was assessed by either seedling extension or dry weight increase. The controls for comparison with the plant extract or leaf leachate treatments were in deionized water, which leaves the possibility that the inhibition was purely osmotic. However, when this has been checked by other workers the osmotic effect has usually been found to be of little importance (e.g. del Moral and Cates, 1971). Species are included in the list only if the difference between treatment and control was statistically significant.

Table I lists 15 species, including monocotyledons, dicotyledonous herbs and trees and one gymnosperm. Some common crop and forage species are

TABLE I

Species which are autotoxic, i.e. whose extracts or exudates significantly reduce growth of their own species

Species	Reference
Plant extract	
Avena sativa (oat)	Nielsen *et al.* (1960)
Zea mays (maize)	
Digitaria sanguinalis (crab grass)	Parenti and Rice (1969)
Dactylis glomerata (cocksfoot)	Grant and Sallans (1964)
Phalaris arundinacea (reed canary grass)	
Lotus corniculatus (birdsfoot trefoil)	
Trifolium pratense (red clover)	
T. repens (white clover)	
Cirsium arvense (creeping thistle)	Bendall (1975)
Helianthus annuus (sunflower)	Wilson and Rice (1968)
Leaf leachate	
Eucalyptus globulus (a dicotyledonous tree)	del Moral and Muller (1969)
Root exudate	
Lolium perenne (ryegrass)	Newman and Rovira (1975)
Hypochoeris radicata (Compositae)	
Grevillea robusta (a dicotyledonous tree)	Webb *et al.* (1967)
Araucaria cunninghamii (a conifer)	Bevege (1968)

included. Among other species which have been tested, some are clearly not autotoxic. For example, among the eight species whose extracts were tested by Grant and Sallans (1964), five were clearly autotoxic (Table I) but *Phleum pratense* was not. Among the eight species studied by Newman and Rovira (1975), *Anthoxanthum odoratum* root exudates were not autotoxic.

This widespread autotoxicity raises the question of why the individual plant does not inhibit its own metabolic processes. One answer is that perhaps it does, to some extent. This is a possible disadvantage of toxin production, together with the metabolic load of toxin synthesis. However, harm to the producer plant may be reduced by three mechanisms.

1. The producer may have unusual metabolic pathways, resulting in it being unaffected by the toxin. Some examples of this are given by Bell (Chapter 6).
2. The toxin may be localized within the cell away from the main metabolic

machinery, for example in the vacuole, or within a few specialized cells in the plant, such as ducts or glands.

3. The substance may be produced only when the plant is specially stimulated, as happens with phytoalexins (see Harborne and Ingham, Chapter 14).

These methods of reducing autotoxicity are familiar with chemicals which provide protection against animals or microbial pathogens but it is less obvious how methods (2) and (3) could operate with allelopathic chemicals. A toxin localized in the vacuole or in special cells can wait for the animal or micro-organism to attack, when it will automatically reach its target; but competing plants do not penetrate each other and need not even come into contact, so the chemical must leave the producer plant to be effective in allelopathy. Glandular hairs provide a mechanism for exuding toxins while keeping the toxin away from most cells of the producer plant. The toxin is produced in cells near the tip of the hair. In some species the cell walls in the hair stalk are impermeable due to impregnation with suberin (Stocking, 1956), and this would prevent the toxin diffusing back through the walls into the main cell mass of the leaf or stem. The toxin passes through the hair's cuticle, often by its rupture and can then diffuse through a water film on the outside of the plant cuticle, or be washed off by rain. While this could cause allelopathy, glandular hairs are not necessarily primarily adapted to it. The film of toxic material could provide an effective barrier to establishment of micro-organisms and a deterrent to insects.

By analogy with phytoalexins, one may ask whether competition stimulates toxin production. If a plant is receiving inadequate quantities of light, water or mineral nutrients due to the presence of another plant, an increased production of toxin might help to keep the competitor from further increase. There are known examples where a reduced supply of light or mineral nutrients causes a very substantial increase in a toxic substance in the plant. Del Moral (1972) and Lehman and Rice (1972) found that deficiency of nitrogen causes large increases in chlorogenic acid (a phenolic) in the stem and leaves of sunflower (*Helianthus annuus*); sometimes the increase is as much as 10-fold. Deficiency of potassium or sulphur also causes increases, though generally smaller (Lehman and Rice, 1972). Reducing the light intensity received by a plant can increase its alkaloid content (Moore *et al.*, 1967). However, deficiencies do not always result in an increased toxin production. Table II summarizes the changes in concentration of two major groups of secondary metabolites which are often toxic, brought about by deficiencies of the requirements for which plants most often compete. The table is based on inadequate data: only one or at most a few species provide the basis for each symbol. Further details are given in Table V. Table II shows that competition for different requirements does not necessarily have the same effect on the

TABLE II

Summary of effects of decreased light intensity, soil water content or supply of major mineral nutrients on the concentration of phenolics and alkaloids in plant leaves or stems

	Effect on plant concentration of:	
Deficiency	phenolics	alkaloids
Light	0	+
Water	0 or −	0 or +
N	+	−
P	?	0
K	+ or 0	?
S	+	?

+, Increase; −, decrease; 0, no consistent change. Further details, and sources of data, are given in Table V.

production of a particular type of chemical: whereas nutrient deficiency usually raises phenolic concentration (in the few species studied), this is not true of shading or water stress. Furthermore, the effect of a particular deficiency on phenolic concentration is often different from its effect on alkaloids. It is thus unlikely that altered toxin levels in response to competition represent a specific adaptation towards increased allelopathic ability; more likely the explanation lies in the metabolic balances of the plant. Alkaloids contain nitrogen, and treatments which increase the plant's total nitrogen concentration may thus increase its alkaloid content. This would explain the effect not only of nitrogen deficiency but of low light, which tends to increase the plant's nitrogen concentration. The increase of phenolic synthesis when nitrogen and sulphur are deficient may arise because phenylalanine is a precursor to proteins, alkaloids and phenolics. Nitrogen and sulphur deficiency would interfere with protein synthesis, and nitrogen deficiency with alkaloid synthesis, thus leaving more phenylalanine available for phenolic synthesis. Light is known to stimulate the primary step in phenolic synthesis, the conversion of phenylalanine to cinnamic acid by phenylalanine ammonia lyase (Smith, 1972), but there appears to be no experimental evidence on whether changes in light intensity within the range likely to be caused by competition would have such an effect. Del Moral (1972) has discussed in more detail the possible significance of changes in toxin levels produced by environmental stress.

Table I has shown that plants can be autotoxic. The question still remains, are the substances more inhibitory to other species than to the producer species? I have collected data from the literature, using experiments where

TABLE III

Effect of extract from shoots of *Medicago sativa* (lucerne) on seedling shoot growth of eight species. Data of Grant and Sallans (1964)

	Seedling shoot length (mm)			
Receiver species	In water (control)	In *Medicago* extract	$\frac{\text{Treatment}}{\text{control}}$	
Medicago sativa	26·2	23·4	0·89	= auto
Trifolium repens	22·0	1·8*	0·08	= allo
T. pratense	38.9	3·8*	0·10	
Lotus corniculatus	27·7	3·8*	0·14	
Dactylis glomerata	34·1	24·3*	0·71	
Bromus sp.	41·6	32·1*	0·77	
Phalaris arundinacea	38·2	38·8	1·02	
Phleum pratense	22·8	24·4	1·07	
	Range of allo		0·08–1·07	
	Mean of allo		0·56	
	Auto		0·89	

* Difference between control and treatment significant ($P < 0{\cdot}05$).

the extract or exudate has been applied to plants of the producer species and at least five other species. Table III shows, for one donor species taken as an example, how the data have been analysed. The degree of inhibition by the extract varied tremendously between receiver species in this example; it is expressed by the ratio treatment/control shown in the right-hand column. All species are included in the analysis whether or not the extract significantly altered receiver growth. When the extract is applied to a species other than the donor species this is termed an "allo" treatment; for these the ratio in the right-hand column ranged from 0·08–1·07, with a mean of 0·56. This may be compared with 0·89 for the "auto" treatment (*Medicago* extract applied to its own species). Thus the auto is above the mean of the allo, but not above all allo; in other words *Medicago* extract is on average less inhibitory to its own species than to the other species tested but it is not less inhibitory to itself than to any other species. Table IV summarizes results for a number of donor species analysed in the same way, including all the suitable data I can find in the literature. Out of the 23 cases, involving 21 species, only two were less toxic to their own species than to any other tested. The clearest feature of the results is the almost symmetrical distribution, with almost equal numbers having auto values above and below the mean of the allo. This is shown also by the means of the allos and autos: since these numbers are below 1 the extracts and exudates are, on average, inhibitory (the root exudates on

TABLE IV

Summary of results of experiments with plant extracts or root exudates, comparing the auto treatment (donor and receiver plants same species) and allo treatments (donor and receiver different species). The method of analysis is set out in Table III and the species and references in Table VI

	Shoot or leaf extract	Root exudate
Number of donor species in which		
(a) auto above any allo	1	1
auto within range of allo, but		
(b) above mean of allo	5	3
(c) below mean of allo	5	3
(d) auto below any allo	2	3
Total	13	10
Mean of all autos[a]	0·663	0·854
Mean of all allos[a]	0·687	0·885

[a] Control = 1.

average less so than the extracts) but the degree of inhibition is virtually the same for autos and allos. In fact the autos are marginally more inhibitory; this is shown also by the greater number of donors with auto below any allo than those with auto above any allo; but with only 23 cases in all, no confidence can be placed in this difference. The clear conclusion is that sometimes plants are less inhibitory to their own species than to others but about equally often they are more inhibitory. There is no evidence that natural selection has favoured plants which are more inhibitory to other species. This suggests that while some species can benefit from allelopathic ability others will be harmed by possessing it and that on average allelopathy is not beneficial to the producer plant. It could be argued that plants with low ability to compete for requirements, for example plants of low stature with little ability to compete for light, would benefit from reducing growth by all plants, including their own species and thus keeping an open vegetation where the intensity of competition is low. However, most of the species of Table IV are herbaceous perennials normally found in closed permanent vegetation (see Table VI), so this suggestion would not apply. If the five annual species are excluded from the analysis the results still show the same symmetrical distribution and the mean of all allos is still marginally higher than the mean of all autos, for both extracts and root exudates. It is even possible to think of situations in which a plant could benefit from allelopathy even though its own species was more inhibited than others, but highly tortuous arguments are involved. The only straightforward conclusion from the data of Table IV is that on average allelopathy is not beneficial to the producer plant.

IV. ARE SPECIES OF STABLE VEGETATION MORE ALLELOPATHIC?

Animals and plants have been classified, according to their ecological strategies, into r- and K-species. r-species are adapted to colonization and early stages of succession; they have efficient means of spread and can grow rapidly, but may not have high competitive ability. K-species are adapted to stable, late succession or climax vegetation; they have high competitive ability but not necessarily high growth rate. It could be that K-species employ allelopathy as part of their competitive mechanism, whereas in r-species it would be less necessary and might be harmful by reducing growth rate through increased metabolic load or autotoxicity. Similar predictions about the distribution of toxic substances in relation to succession, but for a different reason, have been made by Levin (1971), Cates and Orians (1975) and Feeny (1975). They argued that plants of stable vegetation are more easily found by their parasites and predators than those of early succession and so are in more need of protective chemicals.

Cates and Orians (1975) cut discs from leaves of numerous species growing in Washington state, U.S.A., and determined their palatability to two slug species. On average, species from early succession were most palatable, those from late succession intermediate and from climax vegetation least palatable, in agreement with the hypothesis. However, when del Moral and Cates (1971) assessed the toxicity to three receiver species of extracts and volatiles from 40 species in the same geographical area, they could find no relationship between successional status and toxicity. Hartley *et al.* (quoted by Levin, 1976) assayed numerous species of New Guinea for alkaloid content. Among lowland vegetation types, the percentage of species containing alkaloids was among weeds 6·0%, ocean strand species 12·1%, monsoon forest 11·6%, rain forest 21·5%. This agrees with the hypothesis, but is not, of course, a measure of overall toxicity or allelopathic potential.

There seems to be inadequate evidence for deciding whether allelopathy is related to succession. Allelopathy is certainly not totally absent among early colonizers: Rice and co-workers have studied various early colonizers of abandoned farmland in Oklahoma and found evidence of allelopathic ability in many of them (Rice, 1974).

V. ARE SPECIES WHICH LIVE TOGETHER MORE TOLERANT OF EACH OTHERS' TOXINS?

It has been suggested (del Moral and Muller, 1970; Rice, 1974) that species which have coexisted for thousands of years are likely to have adapted to become more tolerant of each others' toxins, compared with species which have only recently begun coexisting. There is evidence that on the strictly local level, tolerance by particular species of a plant's toxins allows them to grow near it or under it. Muller and co-workers have studied the ecology of the shrub *Adenostoma fasciculatum* in southern California. Under the mature shrub few herbaceous species can grow, although nearby on similar soil dense herb growth including many other species can be found. Also, when *Adenostoma* is killed by fire many herbs spring up in the gap. McPherson and Muller (1969) and Christensen and Muller (1975) have presented strong evidence that toxic materials leached out of the leaves by rain are at least part of the reason for poor herb growth under the shrub. Leaf leachates from *Adenostoma* were applied to seeds of various species on filter paper and the germination and radicle extension measured. Figure 1 summarizes the results.

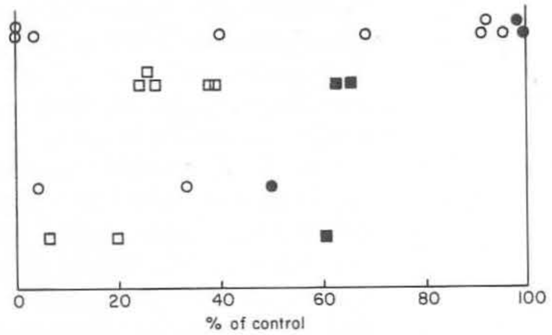

FIG. 1. Response of various species on filter paper to leaf leachate of *Adenostoma fasciculatum*. Circles, germination; squares, radicle extension. Black symbols, species sometimes found under *Adenostoma* in the field; open symbols, species never found under *Adenostoma*, though growing nearby. Upper two lines, data of Christensen and Muller (1975). Lower two lines, other receiver species, leaf leachates concentrated 10-fold, data of McPherson and Muller (1969).

Those species which are found growing under *Adenostoma* in the field were consistently more tolerant of the leaf leachate in the laboratory tests than were the species never found under *Adenostoma*. Thus some species are adapted by their chemical tolerance to the special chemical environment beneath *Adenostoma*. It would be interesting to know whether individuals of these receiver species from outside the geographical area of *Adenostoma* show equal tolerance of its leachate; this would indicate whether their tolerance is fortuitous or the result of direct selection. Not all studies of allelopathy show such a clear correlation between distribution in the field and response to exudate in the laboratory.

In order to find out whether long coexistence in the same area results in species becoming chemically coadapted, it would be necessary to test the

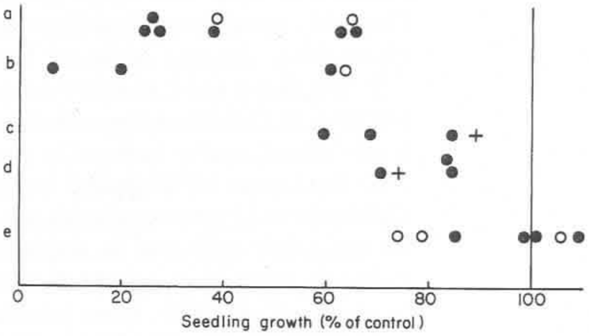

FIG. 2. Response of various receiver species to leaf leachates from four species native to the United States. Each row refers to one donor species, and each point within the row indicates the response of one receiver species. ●, Receiver species native in same geographical area as donor; ○, receiver species introduced and now naturalized in the area of donor; +, receiver is crop species not found in natural vegetation near donor. Donors: a, *Adenostoma fasciculatum* (data of Christensen and Muller, 1975); b, *A. fasciculatum*, leachate concentrated 10-fold (McPherson and Muller, 1969); c, *Quercus marilandica*; d, *Q. stellata* (McPherson and Thompson, 1972); e, *Sporobolus pyramidatus* (Rasmussen and Rice, 1971).

toxicity of a plant's exudate to numerous species, some native to its area, some not. Such a comparison has never been made intentionally but suitable data do exist in the literature. In some studies both native species and species recently introduced but now naturalized have been used as receivers. Sometimes crop species have also been used, thus providing examples of responses by species which have never grown in the same area as the donor. Figure 2 shows the effects of leaf leachates of four species, native to the United States, on receiver species classified as (a) native to the geographical area of the donor, (b) not native there but naturalized following introduction by man, presumably within the last 100–200 years, or (c) crop species. If long coexistence led to plants being more tolerant of each others' exudates, the black spots should be to the right in each row, open circles or crosses to the left. In fact there is no consistent pattern at all, suggesting that the hypothesis is not true. This is supported by other results.

1. Muller and Muller (1956) applied leaf extract from three native shrubs of the Californian desert to seedlings of three native herbs and of tomato. The replication in the data presented is inadequate but, taking the results at face value, the degree of inhibition of tomato was within the range of response of the three native receivers.

2. Muller *et al.* (1964) tested the toxicity of volatiles from crushed leaves of three Californian shrubs, *Salvia leucophylla*, *S. apiana* and *Artemisia californica*, to seedlings of *Cucumis sativus* (cucumber) and of *Avena fatua* which is naturalized in the area. There was no consistent difference between the two receivers in degree of inhibition. However Muller (1966) stated that when

volatiles of these two *Salvia* species and *S. mellifera* were tested against *Cucumis*, *Avena fatua*, three other introduced grasses and two native grasses, *Cucumis* was the least inhibited. No numerical data were given.

3. Del Moral and Cates (1971) applied extracts from 40 species of Washington State to *Pseudotsuga menziesii*, which is native, to *Bromus tectorum* which is introduced, and to barley. On average *P. menziesii* was least inhibited.

4. Hanawalt (1971) applied leaf extracts of *Arctostaphylos* spp. native to California to 12 receiver species, seven native and five introduced. There was no consistent difference in response between the two groups of receivers. However, when Chou and Muller (1972) applied leaf extract of *A. glandulosa* to seedlings of radish, three introduced species and one native, the native species was the most inhibited and the crop species the least.

5. Bevege (1968) applied root leachates from *Araucaria cunninghamii*, *Flindersia australis* and *Pinus elliottii* to *Araucaria cunninghamii*. The degree of inhibition by the pine (which is introduced to Australia) was intermediate between that by the other two species (which are natives).

Among the examples summarized in the preceding paragraph and Fig. 2 only one fits the hypothesis by showing the native species most tolerant of the toxic materials, namely the species of Washington State studied by del Moral and Cates (1971). The opposite situation, with alien species most tolerant is shown by *Arctostaphylos glandulosa*, *Quercus marilandica* (Fig. 2) and perhaps by the *Salvia* species of Muller (1966). In the remaining cases there was no clear difference in response between native, introduced and alien species. The data thus suggest that long coexistence does not result in species becoming more tolerant of each others' toxic exudates.

VI. CONCLUSIONS

This paper has not discussed in detail whether allelopathy operates in the field, but has assumed, on the basis of evidence published elsewhere, that it does sometimes operate. If this assumption is correct, this does not necessarily mean that natural selection has specifically favoured the development of allelopathic ability in plants. Production of toxic chemicals in plants is subject to various selective pressures, depending on: (a) whether the toxic chemical is an intermediate or byproduct of a beneficial metabolic pathway in the producer plant; (b) the effect of the toxin on the producer plant; (c) whether the toxin provides protection against animals or microbial pathogens; (d) whether it reduces growth of competing plants.

The amount of toxic chemical produced will depend upon the outcome of all these selective pressures and allelopathy could occur as a result of chemicals whose primary reason for existence lies elsewhere. Similarly, tolerance of other plants' exudates may depend upon characters such as rooting depth,

TABLE V

Effect of reduced supply of light, water or mineral nutrient on concentrations of phenolics or alkaloids in leaves or stems

Species	Deficiency	Substance	Change in concentration	Reference
		PHENOLICS		
Prunus domestica	Light	Total phenolics	0	Hillis and Swain (1959)
Triticum aestivum	Water	Various phenolics	0 or −	Tsai and Todd (1972)
Nicotiana tabacum	N	Chlorogenic acid	+	Wender (1970)
Helianthus annuus	N	Chlorogenic acid	+	del Moral (1972) Lehman and Rice (1972)
		Isochlorogenic acid	+	
		Neochlorogenic acid	+	
		4-*O*-caffeylquinic acid	+	
	K	Chlorogenic acid	+	Lehman and Rice (1972)
		Neochlorogenic acid	0	
		4-*O*-caffeylquinic acid	0	
	S	Chlorogenic acid	+	
		Neochlorogenic acid	+	
		4-*O*-caffeylquinic acid	+	
		ALKALOIDS		
Phalaris tuberosa	Light	Tryptamine alkaloids	+	Moore *et al.* (1967)
	N	Tryptamine alkaloids	−	
	Water	Tryptamine alkaloids	(+)[a]	Williams (1972)
Phalaris arundinacea	N	Total basic alkaloids	−	Marten *et al.* (1974)
	P	Total basic alkaloids	0	
Lolium perenne	N	Perloline	−	Bennett (1963)
	P	Perloline	0	
Festuca arundinacea	N	Perloline	−	Gentry *et al.* (1969)
	PK	Perloline	(+)	

+, increase; −, decrease; 0, no consistent change; ( ), small change.

[a] Only if water stress severe.

Note: Anthocyanins are often increased in high light intensity (Blank, 1958) and anthocyanidins by N and P deficiency (Davies *et al.*, 1964) but they have not been included because their relevance to allelopathy is uncertain.

cuticle thickness, cell membrane properties and the relative importance of alternative metabolic pathways, which are subject to other selection pressures. I have tried here to test two hypotheses, firstly that natural selection has favoured ability in plants to reduce the growth of their competitors by allelopathy; secondly, that natural selection has favoured the development in plants of tolerance to toxic chemicals produced by other species which they

TABLE VI

Details of experimental results upon which Table IV was based

Species	Material tested	No. of receiver species	Result[a]	Reference
Bromus sp.	Shoot extract	8	+	Grant and Sallans (1964)
Dactylis glomerata	Shoot extract	8	− −	
Phalaris arundinacea	Shoot extract	8	+ +	
Phleum pratense	Shoot extract	8	+	
Lotus corniculatus	Shoot extract	8	+	
Medicago sativa	Shoot extract	8	+	
Trifolium pratense	Shoot extract	8	−	
T. repens	Shoot extract	8	−	
Avena sativa	Shoot extract	6	−	Nielsen *et al.* (1960)
Zea mays	Shoot extract	6	−	
Digitaria sanguinalis	Whole plant extract	6	−	Parenti and Rice (1969)
Cirsium arvense	Leaf extract	7	− −	Bendall (1975)
Helianthus annuus	Leaf extract	9	+	Wilson and Rice (1968)
	Root exudate	9	−	
Sporobolus pyramidatus	Root exudate	7	−	Rasmussen and Rice (1971)
Anthoxanthum odoratum	Root exudate	8	+	Newman and Rovira (1975)
Cynosurus cristatus	Root exudate	8	+	
Holcus lanatus	Root exudate	8	+	
Hypochoeris radicata	Root exudate	8	− −	
Lolium perenne	Root exudate	8	− −	
Plantago lanceolata	Root exudate	8	− −	
Rumex acetosa	Root exudate	8	−	
Trifolium repens	Root exudate	8	+ +	

[a] + +, Auto above any allo; +, auto within range of allo but above mean of allo; −, auto within range of allo but below mean of allo; − −, auto below any allo.

commonly grow with. These hypotheses in turn give rise to three others which I have been able to test against data in the literature: (1) that plants are on average more toxic to other species than to their own species; (2) that competition for basic requirements results in increased toxin production; (3) that species which have grown together for thousands of years are more tolerant of each others' secondary chemicals than those which have not. In each case the actual data show a random distribution with respect to the hypothesis, sometimes supporting it but equally often in the opposite direction. This strongly suggests that there is not often specific selection for allelopathic ability or tolerance of allelopathy but that these plant properties are better viewed as the fortuitous outcome of characteristics of the plant whose primary reason for existence is not allelopathy. This is not to deny that allelopathy occurs, nor to imply that it has negligible ecological significance, but rather to suggest that it is not always beneficial to the producer plant and that it should not be viewed in isolation from the other ecological implications of plant secondary metabolites.

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